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THE ANOLES OF THE EASTERN CARIBBEAN
(SAURIA, IGUANIDAE)

Parts IV-VI

BY JAMES D. LAZELL, JR.

and

ERNEST E. WILLIAMS

WITH THREE PLATES

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No. 9 — *The Anoles of the Eastern Caribbean (Sauria, Iguanidae) Parts IV-VI*

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IV. THE ANOLES OF THE NORTHERN LEEWARDS, ANGUILLA TO MONTSERRAT: NEW DATA AND A NEW SPECIES.

By ERNEST E. WILLIAMS

INTRODUCTION

Initially, as I have stated in the preface to the first part of this series (Williams, 1959), I felt that the Museum of Comparative Zoology collections provided an adequate survey of the anoles of the Lesser Antilles. We had relatively large series of most of the forms recognized, and representatives of all. Many of the specimens were types or syntypes of Garman's or Barbour's names. There were indeed doubts about the application of certain older names, but this was felt to be a purely nomenclatorial problem that could wait upon an opportunity to solve it. There appeared to be very plausible grounds for the belief that a very satisfactory beginning in the revision of the *Anolis* of this limited region could be made by a study of the collections of this one museum — a museum that had a tradition of interest in the region.

As it has worked out, this belief has proved quite wrong. Basic to this error was an assumption that has proved fallacious: the assumption that these small islands could harbor but one or, at a maximum, two species of *Anolis* per island. Where there were as many as two, Barbour had already provided a neat categorization that seemed also an explanation: there were a rupicolous and an arboricolous series.

Underwood (1959) has commented on the taxonomic philosophy of Garman and Barbour which reasoned from the reality of distinct forms on some islands to the existence of endemics on every island. But neither he nor I at the beginning questioned the assumption of extreme faunal restriction and minimal faunal differentiation.

I have now had the opportunity to study many specimens not available to Underwood in the summer of 1957. I have examined the material at the American Museum of Natural History as well as material from the Chicago Natural History Museum, the University of Michigan Museum of Zoology, and also United States National Museum specimens seen by Underwood briefly or not at all. I have received for determination the anoles collected by Walter Auffenberg and J. Wayne King in the Leeward Islands in the summer of 1958. Specimens from Antigua, Montserrat, and Dominica collected in 1958 have been donated to the MCZ by James D. Lazell, Jr. (Over 500 anoles were collected on Dominica by Lazell in 1959. He here publishes separately on the anoles of this island.) Previously I had received live specimens sent up by Underwood in the course of his collections. Kodachromes of some of these are at hand, as well as kodachromes prepared by J. Lazell, Jr., and notes on color in life by Wayne King, Underwood, Lazell, Proctor and others have been available. Live and preserved anoles collected by G. R. Proctor have been repeatedly donated to the MCZ via Underwood. In 1961 National Science Foundation Grant NSF-G16066 provided funds for a Caribbean tour which permitted me to see in the field *Anolis trinitatis*, *A. roquet aeneus*, *A. roquet roquet*, *A. bimaculatus leachii* and *A. wattsi*.

This quantity of previously unreported material supplements Underwood's (1959) presentation, restoring certain names abandoned by him, adding new forms, and hinting at complications still to be recorded. It may be true that the Lesser Antilles provides us with the simplest segment of the genus *Anolis* but this, if it be true, promises tasks in other areas formidable to the point of fantasy. What is here provided is a continuing progress report.

THE *bimaculatus* GROUP ON THE NORTHERN ISLANDS

Basically the situation seems clear and neat for the members of the *bimaculatus* group in the northern islands from Anguilla to Montserrat. Each bank of the Leewards supports a single

form of the *Anolis bimaculatus* group, and each form is unmistakable on color alone. "Color" is here understood to be color in life; preservation in strong formalin reduces the varied shades present in life to an undistinguished and unpleasant brown and destroys all but the most prominent patterns. Even alcohol loses much of the colors of life and may retain one only—and that not the most frequent—of a repertoire of patterns possible to each individual of a species. I here summarize the presently available evidence for all representatives of the *bimaculatus* group south to Montserrat. I include at the end of each discussion some remarks on the few distinctive scale characters of the several forms, since these were not stressed by Underwood in his presentation; these scale characters are few indeed and modal rather than absolute. I have employed for each form the trinomials used by Underwood, although I have lingering doubts that e.g. *gingivinus* is really conspecific with *bimaculatus*. I find in the case of these island forms, for which the test of sympatry or parapatry is unavailable, the arguments for "splitting" as little compelling or persuasive as those for "lumping." The conventional standard of the degree of difference of valid sympatric forms does not apply in *Anolis*. Forms that in morphology and color are quite distinct may intergrade; forms that are just distinguishable may be full species. I regret that Linnean nomenclature compels decisions which the evidence cannot warrant.

Anolis bimaculatus gingivinus

Notes are available on colors in life for *gingivinus* both in Anguilla and St. Martin. For Anguilla there are notes by both Auffenberg and King on their own collection and also by Underwood for three specimens sent him by G. R. Proctor. I collate their remarks below; I have ventured to combine their slightly varying remarks the more confidently since anoles differ not only from individual to individual but from moment to moment.

Ground color of dorsum dark brown to gray, the gray streaked and spotted with brownish gray or dark brown or with obscure diamonds dorsally. A white or gray stripe from neck above to hind leg. Tail banded with light and dark, sometimes with bronzy sheen at base. Venter light brown or gray. Orbital scales dark brown. Iris black. Dewlap deep yellow orange to amber.

King's description is the only one at hand for St. Martin. He found the *gingivinus* there very similar to Anguilla specimens except that "one was a pale green; none of the Anguilla anoles ever assumed a green color."

This interesting difference in color repertoire may possibly be correlated with a behavioral difference that King noted. For Anguilla, he states: "I noticed a lack of anoles in the trees and bushes — the anoles that I see are always on the rocks or scurrying through the brush. . . . I collected anoles on the hillside north of the salt pond. Almost every large rock not surrounded by weeds had an anole sunning itself on it. The rocks seem to provide the anole with a good view of the surrounding area for they all darted behind the rock no matter what side they were approached from."

In St. Martin, on the other hand, King very specifically mentions catching anoles "from the rocks and trunks of trees." Queried as to this point, he is quite emphatic (letter of March 1, 1959): "Both Dr. Auffenberg and myself feel that the anoles on St. Martin are more arboreal than those on Anguilla. On St. Martin I collected them in trees, bushes and on rocks. To my knowledge I didn't collect a single anole on a tree or bush while on Anguilla. Although I rather doubt it myself, this may be a reflection of the numbers of available trees — Anguilla is very, very scrubby."

The middorsal scales are strongly enlarged in all *gingivinus*, almost as prominent as in members of the *wattsi* group, but in contrast to the conditions in the latter the ventrals in *gingivinus* are quite smooth.

Anolis bimaculatus sabanus

No fresh or live material of this form has come to hand. In this animal, however, the preserved specimens probably give a fairer image of color in life than is true in any other case. The very bold well-spaced spotting (dark brown on light, almost regular), the absence of any flank stripe, and the white belly color are well shown in the alcohol preserved types in the MCZ. The extreme boldness of the pattern is absolutely distinctive, not approached by any other *Anolis*.

There is no enlargement of the middorsal scales in *sabanus*; the ventrals are smooth.

Anolis bimaculatus bimaculatus

I collate below Auffenberg's and King's notes on the color in life of Nevis *bimaculatus*.

Ground color of dorsum yellow green. Flank stripe green or yellow, rarely white. Tail gray or green (blue green) with at

least indications of darker crossbands. Venter yellow white. Head pastel blue or blue green, upper labials and neck yellow. Orbital skin green or light yellowish green. Iris black. A black spot usually present just over front limbs. Dewlap light yellow.

Miss Cochran's (1934) description of a St. Eustatius animal from color notes by Dr. Paul Bartsch is more elaborate:

"The top of the head in front of the eyes is peacock-blue, the larger scales with a pinkish flush that becomes intensified behind the eyes and on the temporal region. The pineal eye is gray brown. The side of the head anterior to the eyes is peacock blue. The area about the eyes is intense brilliant green. The top of the nape is blue with a pinkish flush. The main dorsal part of the body is yellowish green from the nape to the tail. This color extends from the base of the tail over the fore and hind legs, but these have a yellowish pink superimposed, which gradually fades into yellow-green on the belly. On the throat, and from there to the fore leg, are irregularly distributed spots of orange, the posterior portion being uniform in color. The inside of the legs corresponds in color with the belly. The posterior half of the upper side and the outside of the hind legs are marked with obscure spots of blue. An inch behind the base of the tail the same peacock blue seen on the forehead reappears, slowly grading from the general dorsal color. The last two inches of the tail are pale brown. Here spots and splashes of dark brown, blue, and various shades of rose are irregularly scattered about. The median under part of the tail is a little paler than the ground color of the rest, and free from spots on the outer half, the posterior inch of the coarse scaled portion being brown."

Miss Cochran quotes Dr. Bartsch as remarking of Nevis caught *bimaculatus*: "—the blue-green one here is not so beautiful as on St. Eustatius."

King's comments on St. Kitts animals indicate local difference here also: "The yellow shoulder stripe in these lizards is very intense and we saw none in which the stripe was white as in some of the Nevis specimens. They are very large here, some reaching a foot in length and are bluer on the head and tail than the Nevis ones." Underwood has commented that St. Kitts animals are chalky green rather than blue green and that creamy markings are more extensive on the head.

Miss Cochran has commented that the Nevis specimens available to her lacked the shoulder spot characteristic of the animals from St. Eustatius and that the St. Kitts specimens were intermediate — the spot slightly apparent. The reduction or absence

of the shoulder spot in Nevis specimens is very well borne out by the preserved specimens in the MCZ as is the small size of the shoulder spot in St. Kitts specimens. On live Nevis specimens Auffenberg comments, "the large males have a black spot on the body just over the front limbs — however this is quite variable." King states: "There are black spots dorsally and laterally on the back and hind legs and tail. These spots are present only in large males, absent in small ones. Just dorsal to the white shoulder stripe there is a large black spot about the size of the ear opening — one on each side."

In regard to spotting, other than the shoulder spots, preservation produces results very difficult to interpret. In some series the specimens are rather consistently flecked with discrete small spots all over the dorsal surface of head, body and tail. In other series from the same island spotting is inconspicuous or absent. Some formalin preserved specimens show transverse markings and mottlings or even very erratic discolorations. Important as color is in the taxonomy of *Anolis*, it must be used with discretion.

The middorsal scales are somewhat enlarged and sometimes swollen in *bimaculatus* but grade quite gradually into the flank scales. The ventrals are always smooth.

Anolis bimaculatus leachii

Auffenberg provides a color description for *leachii* from Antigua: Ground color light bright green. Tail greenish at base fading into greyish brown over most of its length. Head greyish to brownish speckled or mottled with dark brown or black, "this pattern extending over the shoulders and entire dorsum of some specimens." Dewlap yellowish orange.

Preserved specimens show considerable variability in dorsal speckling and vermiculations. As Underwood has indicated, the spotting tends to coalesce to vermiculations anteriorly but remains discrete posteriorly. Half grown animals appear to show at least occasionally bolder spotting than large adults, but in all cases with much individual variation. (Formalin preservation emphasizes the spotting more than does alcohol preservation; in life also the same individual will show bolder or less bold spotting in different phases.) Sometimes the spots coalesce more or less longitudinally to give the impression of broken lines. In all cases, however, the lower flanks in front of the thighs show no vermiculations and minimal spotting.

Large males have the middorsal scales very distinctly swollen and noticeably but not greatly larger than the adjoining scales. The ventrals are usually smooth.

Anolis bimaculatus nubilus

I have had the opportunity to examine freshly-preserved specimens of this form collected for the United States National Museum. There is, however, no color description from life.

From the preserved animals it is evident that the characters noted by Underwood — almost no trace of flank stripe and light speckling most pronounced in the hind limbs — hold good in the new material. This form seems quite peculiar and distinct in that, at least in preservative, speckling appears to be almost confined to the hind quarters. This is in strong contrast with the Antiguan animal which both in life and in preservation is vermiculate anteriorly — i.e., the speckles are there confluent — and in which even the speckling is reduced posteriorly. The Redonda form is equally different from the Desirade animal in which in all preserved specimens vermiculation is present both anteriorly and posteriorly. The fresh Redonda specimens differ also from the Desirade specimens in the absence of any bright pigment on the orbital scales. In Redonda animals of a general tan body color, these scales are blue gray as preserved.

On the evidence of the new material there is no doubt that the Redonda form is as distinct as is any of the other *bimaculatus* color races, but the lack of knowledge of color in life makes the comparisons incomplete.

The middorsal scales are distinctly larger than the lower flank scales but grade quite gradually into those alongside them. The ventrals are smooth.

Anolis bimaculatus lividus

Underwood has very well described this form. I quote his description with the color variations (or differences in interpretation?) noted by Auffenberg and King in brackets.

“The predominant color is bright yellow green [bright green, pea green] grading to blue [blue green, light blue; “the intensity of the color makes it appear almost fluorescent”] on tail. There is russet [bright orange, red orange] around the eye and a variable extension of russet [brownish, yellowish brown, rust brown] onto the head and forequarters. Oblique rows of pale spots were sometimes present on the sides. The belly is yellow [light yellow to white]. The flank stripe is never strongly defined and is very variable in its extent. These lizards can turn a warm brown [uniform brown, olive]. The fan is light ochre

[light yellow to orange].” The pale spots on the sides show in a few of the specimens preserved by King. Whether this is a constant character of some specimens or a phase that any individual might sometimes assume, I do not know.

The middorsal scales tend to be enlarged and swollen. The ventrals are weakly keeled.

THE *wattsi* SERIES

Specimens of a small anole with strongly keeled ventrals, the keels in line and with two middorsal rows enlarged, are known from Anguilla, St. Martin, St. Eustatius, Nevis, Barbuda and Antigua, unknown on Saba, St. Barts, Redonda, Montserrat, or any isle to the south except for St. Lucia, where this form has only recently been discovered in the port city of Castries (Underwood, 1959, p. 217).

Two nominal species have been described in this series: *A. wattsi* Boulenger 1894 (type locality: Antigua), *A. forresti* Barbour 1923 (type locality: Barbuda). Underwood (1959), without discussing the matter, has placed *forresti* in the synonymy of *wattsi*. In this action he appears to be fully justified; the characters cited by Barbour (1923) in the type description do not hold, and no other characters to distinguish *forresti* and *wattsi* have been found.

Synonymy of *wattsi* and *forresti* is not surprising. The two type localities — Barbuda and Antigua — are islands of one bank with similar ecologies. Underwood was unable (as I am also) to distinguish between the *bimaculatus* representatives on these two islands.

It was somewhat more surprising that the animals from Anguilla, St. Martin, St. Eustatius, St. Kitts and Nevis appeared to be the same as those from Barbuda and Antigua. This was at variance with the situation in the *bimaculatus* group in which each bank had its own well marked form. However, Underwood had seen both the Antiguan and St. Kitts populations in life and had found only trivial color differences. It seemed clear, therefore, when Underwood wrote that *wattsi* was a single form which had undergone hardly any differentiation on the several islands and banks that it inhabited. Underwood, indeed, used *wattsi* as his illustration of “the process of colonization of a group of islands.” He said, “we have the absence from the southeast (i.e., the southern Lesser Antilles) and the slight measure of differentiation between the islands as evidence of relatively recent arrival from the west.”

This conclusion seemed at the time of its writing as plausible to me as to Underwood. It was, therefore, a very real surprise when Auffenberg and King discovered in Barbuda a second species of the *wattsi* group.

Derby Cave, the area in which the new species was first found, was an extremely peculiar habitat — a sink hole in the limestone highlands to the east of Codrington, Barbuda. Wayne King has vividly described the sink hole and its environs:

“The area surrounding the sink hole is scrubby — seldom reaching over twenty feet — woods. Cactus, both “organ pipe” types and low rambling “Opuntia” types are plentiful. Most of the trees and bushes are thorny. There are numerous outcrops of limestone in the area, and very little soil except in

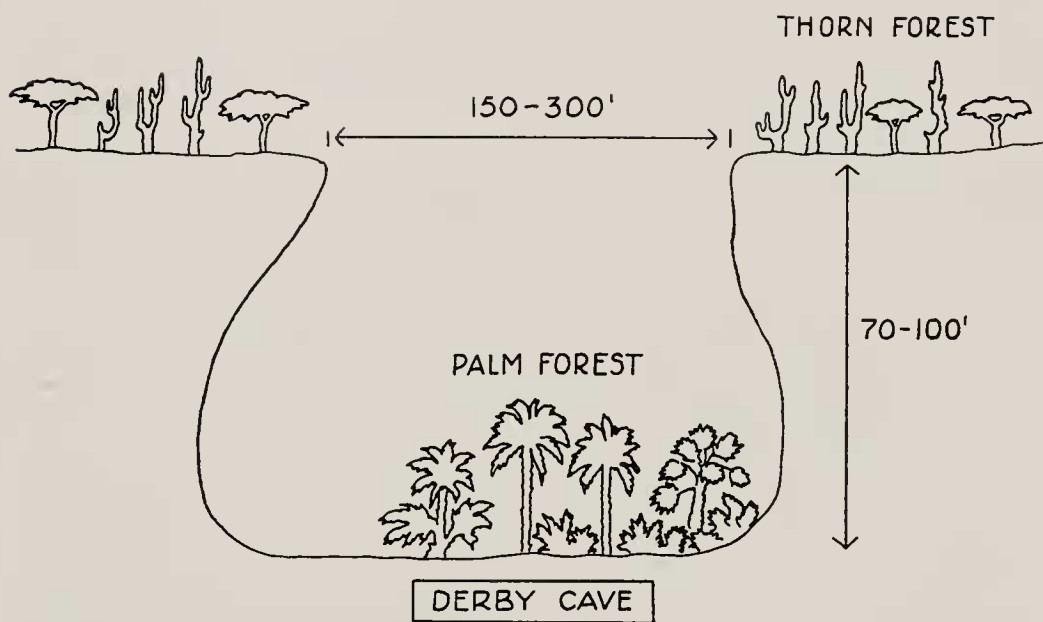


FIGURE 1. Sketch (after field sketch by Walter Auffenberg) of the ecological situation at Derby Cave, Barbuda.

pockets between the outcrops. The sink measures roughly 100 yards across and 80 feet deep. The south side is a sloping pile of rock and rubble; this is the only side which can be used to enter the sink. The other sides, in particular the north side, are sheer drops to the bottom. The north side is overhanging. The bottom of the sink is a loamy clay, dark brown to red in color. There is a dense stand of trees in the bottom. The dominant tree is a palm very similar in appearance to the cabbage palm of Florida, except it is very slender. The trunk of the palm is seldom over six inches in diameter, but trees may be 40 feet tall.

There are many small palms — young ones. Another tree which is abundant is a *Ficus* — growing mainly on the rock slope on the south side of the sink. The top of the sink is about 150 feet elevation."

It was on the trunk of the palms that the new species was taken. It was immediately recognized as distinctive on color alone. I compare in parallel columns the color of Barbuda and Antigua *wattsi* and the new species.

*wattsi**new species*

Dorsum greenish brown to brown but base of tail and most of its length translucent yellow or light orange.

Dorsum uniform dark gray or brownish gray or brown to drab olive green.

Top and sides of head including orbital scales translucent yellow or light orange but temples blue gray.

Head without yellow, orbital scales green. No blue gray on temples.

Hind limbs without red markings.

Thighs with red or rusty bands which on the posterior aspect are free of dark overlay and thus appear as brilliant orange spots.

Belly bright yellow.

Belly not yellow.

Dewlap yellowish orange.

Dewlap light green.

The new species was later seen or taken at other localities on Barbuda and Antigua:

1. Dark Cave, 6-7 mi. SE Codrington, Barbuda: anoles seen in shallow sink in which the cave occurs.

2. Bryant Cave, 6-7 mi. SE Codrington, Barbuda: a large sink similar to Derby Cave with a pool of ground water at bottom.

3. Gaynor's Mill, 1 mi. W, 1½ mi. S. Willikies Village, St. Philip's Parish, Antigua: a thick growth of trees with a high canopy growing on the broad flood plain of the river that empties into Nonsuch Bay.

The specimens from these localities differed from those from Derby Cave where the form was first found only in having *white* rather than *red* spots on the posterior edge of the thighs.

The two additional Barbuda localities closely resemble Derby Cave; the Antigua locality is similar in its dampness, high trees and shade.

The color (especially dewlap color) and habit differences reported by Auffenberg and King are in themselves adequate to diagnose the new species. However, the color differences have wholly disappeared in the preserved specimens before me. I have, therefore, strenuously endeavored to find scale differences. I have not been able to find them. Nevertheless, I regard the species status of the new form as unquestionable. Maintenance of sharp color difference, including dewlap color difference, in several small, isolated colonies is for me clear evidence that gene flow does not occur.

As the newly discovered member of a species pair, the new species may receive a Latin name meaning the other one of two and is thus called:

ANOLIS ALTER sp. nov.

Type: UF¹ 12457; Derby Cave.

Paratypes: UF 12458-1,2,3,4; MCZ 64345-8, same data.

Referred specimens: UF 12459, Bryant Cave; UF 12460, Gaynor's Mill.

Diagnosis. Closest to *A. watti* Boulenger but differing in the absence of yellow on snout and tail, in having a green rather than an orange-yellow dewlap. Differing as well in habitat, being confined to moist shaded areas instead of open dry conditions.

Description. Head scales smooth or at most weakly keeled. Five to seven scales across head at level of second canthal. No frontal depression.

Supraorbital semicircles broadly in contact, partially separated from the supraocular disks by one row of granules on each side. Supraocular disks consisting of *ca.* 5 enlarged scales, separated from the series of overlapping supraciliary scales by 3 rows of keeled subgranular scales. Canthus sharp, canthal scales 5, the first largest, decreasing regularly anteriorly. Loreal rows 4. Temporal scales very small, smallest in center, bounded above by a moderately distinct double line of supratemporal scales. Interparietal slightly smaller than ear, separated from the supraorbital semicircles by two scales, flanked laterally and posteriorly by scales markedly larger than the body scales.

Anterior frontal moderate but less than half the size of anterior supraorbital, separated from the first canthal scale by one scale a little larger than itself.

¹ Florida State Museum, University of Florida, Gainesville.

Four suboculars in contact with supralabials, the subocular series not continued behind the eye, continued forward by two large scales and meeting canthal ridge with no smaller scales intervening. Five to six supralabials to center of eye.

Mentals a little longer than wide, three small granules inserted between their posterior tips. Only one sublabial on each side in contact with the infralabials. Central throat scales small, cycloid, keeled.

Two middorsal rows enlarged, keeled, less than twice adjoining scales which grade gradually into keeled flank scales. Ventrals much larger, keeled, imbricate. Enlarged postanal scales present.

Dewlap scales as large or a little larger than ventrals, keeled, closely packed.

Scales of upper and lower limbs unicarinate, of digits multicarinate. *Ca.* 17 lamellae under phalanges 2 and 3 of fourth toe.

Tail compressed with a strongly enlarged middorsal row of enlarged scales, three per verticil. Lateral scales keeled, large, in 4-5 rows. Ventrally 3 pairs of scales per verticil, somewhat enlarged.

Size: Type, 42 mm snout-vent length.

Comment. Squamation in the *wattsi* group is not by any means uniform. There is variation in the size and crowding of the middorsal enlarged scales, in the degree of keeling, and, to a less degree, in the size of the ventrals. There is also evident variation in the size of the flank scales.

None of these characters, however, appears to be fully useful taxonomically. The size and crowding of the middorsal scales is a sexually dimorphic character: the adult males and females of typical *wattsi* may be accurately sexed by examination of the middorsal scales alone. At one time it seemed possible that *alter* might be distinguished by the less swollen, smaller middorsal scales of the males, more similar to those of females, than in *wattsi*. However, there is a size factor in this sexual difference and when the smaller males of *wattsi* are compared with the available males of *alter* the difference, while probably still real, becomes so subtle as to approach invisibility. The largest male of *alter* is only 42 mm; males of *wattsi* approach 50 mm. There may be a real difference in maximum size here, but the material does not exist to demonstrate the point.

Some of the Nevis specimens of *wattsi* collected by King are near maximum for the species and yet appear to have markedly

smaller middorsals and small flank scales and less keeled ventrals than Antiguan specimens of the same size. Other Nevis specimens, smaller in size (MCZ 38375-6), have significantly larger middorsals and larger flank scales and well keeled ventrals. It is possible that distinct forms are here being confused but without additional information I am compelled to regard the differences as "individual variability."

Color, thus, seems to be the only useful character; the colors in this instance are not likely to be saved even by preservation in alcohol rather than in formalin. Reds and yellows are notoriously fugitive in alcohol and are retained only for a limited period in formalin. The spots on the hinder side of the thighs so much emphasized in the descriptions of live *alter* by King and by Auffenberg are present in all members of the *wattsii* group; they are apparently merely less conspicuous in brown and yellow *wattsii* than in green and red or green and white *alter*. In preserved specimens there is no perceptible difference. A blue tinge appears on the temporal region of Antiguan and Barbudan *wattsii*; this is absent in the *wattsii* of the St. Kitts-Nevis bank. It will, even in preserved specimens, assist in the recognition of *alter* as compared with sympatric Antiguan-Barbudan *wattsii*.

We are left, therefore, with no secure means of telling all preserved *alter* from all preserved *wattsii*. For identification we need data on ecology and on color in life. These are thus true sibling species — since "sibling," here as always, means difficult to tell apart by the *conventional* methods of the taxonomist.

I would, indeed, lack the courage to describe *Anolis alter* if I had not renewed my acquaintance with live *wattsii* by a visit to Antigua in December 1961 and if Walter Auffenberg had not procured for me live *alter* from Derby Cave in March 1962. The color differences which I have listed above for these two species (p. 462) are fully confirmed. The orange so conspicuous on snout, chin, tail and dewlap in live *wattsii* is quite absent in live *alter*. The sole difference which the new collections reveal is that the red spots on the thighs cited for topotypic *alter* in the collections made in the summer of 1958 are in the March-caught specimens of 1962 dull orange. This difference may reflect seasonal changes. At all events it only slightly diminishes the clear-cut difference between the two forms, and is all the less important since *red* markings on the hinder side of the thighs are always absent in non-topotypic *alter*.

V. GEOGRAPHIC DIFFERENTIATION IN *Anolis oculatus*
ON DOMINICA

By JAMES D. LAZELL, JR.

In 1956 Garth Underwood collected two series of *Anolis oculatus* in Roseau. Examining these and the specimens already in the Museum of Comparative Zoology he was led to suspect local population differences and therefore concluded in his report (1959) on the anoles of the eastern Caribbean that "clearly Dominica will require further careful examination."

In June of 1958 I was in Dominica specifically for the purpose of collecting some of the larger reptiles for the Philadelphia Zoological Gardens. At that time I collected a number of anoles at several different localities and noted striking differences in these series, apparently correlated with climate and elevation. This collection was donated to the Museum of Comparative Zoology and the following year I returned on behalf of that institution to determine what geographical differences existed and what the relationship of the apparent forms might be. In the course of eight weeks I collected over 500 specimens of this species from thirty localities; it now seems clear that in fact only one species is present but that it divides into four strikingly distinct geographic races.

Anolis oculatus is clearly a member of the *bimaculatus* group of Lesser Antillean anoles. (I follow Underwood [1959] in treating it as a distinct species.) It averages much smaller than *bimaculatus* (adult males: 70-76 mm snout to vent — except in the upland race, which approaches *bimaculatus* with lengths of up to 96 mm), and possesses weakly keeled ventrals and a double row of enlarged, sometimes swollen, middorsal scales. Generally the scales are convex, particularly on the head and neck. All forms show caudal cresting in the adult males and in some this is pronounced. Males also have an extensible nuchal crest.

Coloration and pattern vary widely within the species and furnish the principal basis for differentiation of the forms. The species as a whole shows a greater or lesser amount of spotting; from this feature the trivial name is derived. The spotting consists of alternating primary and secondary vertical rows of light spots — generally three to five of each along each side of the animal. The primary rows have their spots accentuated by dark, often black, pigment areas in the adult males; these dark pigment areas may be borders on several primary spots, or dots

or flecks surrounding or adjacent to a few primary spots, or large black patches forming a background for a number of primary spots and extending so as to nearly include the secondary rows. In one form the dark pigment areas may be occasionally completely lacking; in general this dark pigmentation is more pronounced on the larger male specimens and absent completely on the young and the half grown.

In ecology and habits *A. oculatus* seems plastic. It utilizes almost any available habitat from sea level to nearly 3000 feet. It appears, however, to be much more common in some areas than others. Along the Trans-Insular Road between Bells and Concord, for example, a distance of some ten miles, repeated trips resulted in the capture of only one specimen. In the same type of habitat and at similar elevations in other areas I had no trouble securing series. From just south of Roseau and just south of Point Mulatre an imaginary line can be drawn, south of which any anole is hard to come by, whatever the elevation or habitat one seeks them in. Why anoles should be so abundant in places like Roseau, the Fresh Water Lake, the Cabrits or Woodford Hill — each locality possessing a different form — and so scarce in certain other localities I leave to further investigation. Generally, however, the species is abundant enough so that several series of each form could be taken without difficulty and intermediate populations collected also.

This is a lizard with a preference for only vertical stations; it does forage on the ground and seldom ascends to a height of more than a few yards, but it seems to prefer sitting on a vertical substrate — whether it be a tree, bush, wall, road-cut, stone or building. It will occasionally seek shelter under stones, or between them, or in root masses if pursued. Further discussion will be found under the subspecies. (For distribution of subspecies see map, Plate 3.)

ANOLIS OCULATUS OCULATUS (Cope)

Xiphosurus oculatus Cope, 1879. Proc. Amer. Phil. Soc. 18: 274.

Cotypes: USNM¹ Nos. 10139-48, 10150-1, 10153. Type locality, Dominica.

Coll. Ferdinand Ober.

Cope's description does not mention a definite locality within the island, and the type series contains specimens that show occasional similarities to the northern Leeward coast form. Perhaps

¹ United States National Museum.

Ober's collection is composite, or represents an intermediate locality. However, most of the specimens described by Cope fit reasonably well with the southern coastal form, and some, like USNM 10145, closely resemble our figure of MCZ 60364 from Roseau. Thus it seems advisable to restrict the type locality to Roseau, the principal seaport of the island. The following is a description of fresh material collected by me.

Diagnosis. Ground color olive to tan; venter dirty yellow to whitish. Spots, both primary and secondary rows, less distinct than in any other form and sometimes completely lacking. Black pigmentation adjoining spots very reduced or absent.

Coloration in life of adult males. (MCZ Nos. 60359-408, Roseau; coll. J. Lazell, 8 August, 1959.) Extremely variable; most specimens mottled olive or tan with dirty yellow venters and a yellowish tinge on the sides. Most specimens show at least a few spots in the primary rows; these are indistinct and show up best when there are black flecks or patches surrounding them; these patches occur in the majority of specimens around one to two, occasionally three, primary spots. In some specimens there is no black pigment present and in a few the primary spots have become so indistinct that the animal appears solid colored. The secondary spot-rows are generally faded to mere mottling between the primary rows. There is little if any marking on the head and neck and no distinctive coloration on the skin around the eye. (Top, Plate 1.)

Throat fan. Pumpkin yellow to orange.

Color of females and juveniles. Light olive to tan with whitish venters. Spots, if present at all, are very indistinct. There is usually a distinguishable dorsal stripe and often a lateral streak.

Additional series. MCZ Nos. 60425-40, Second Layou River Bridge, above Hillsborough; MCZ Nos. 60350-8, Hillsborough; MCZ Nos. 60409-14, Pointe Michel; MCZ Nos. 60415-24, Grand Bay. All of these specimens agree on all characters except that in the Grand Bay series there are no large adult males and no specimens showing any dark pigment areas.

Discussion. The southern leeward coast of Dominica is semi-xerophytic; this zone rounds the southern tip of the island and extends northward as far as the 1600 foot barrier of Morne Paix Bouche. This mountain, placed exactly on the coast, separates the drier area to the south from the wet lowlands or transitional forest of the windward coast to the north. Thus it is from just south of Morne Paix Bouche, around the southern tip and then

northward to the Layou Valley, that the nominate form of *Anolis oculatus* occurs. MCZ Nos. 60683-4, from Morne Paix Bouche, are almost typical *oculatus*; they differ somewhat in having more spotting than is usual and a richer, browner ground color. Thus I have considered them intergrades with the form of the more northern windward coast.

Caudal and nuchal crests are present in *A. o. oculatus*, but less evident than in any other form.

This is the smallest subspecies, the largest male measuring 73 mm snout to vent.

ANOLIS OCULATUS CABRITENSIS subsp. nov.

Type. MCZ No. 60245, the Cabrits (= Prince Rupert Point), northwest of Portsmouth, Dominica. Coll. J. Lazell, 8 June, 1959.

Diagnosis. Ground color grey to pale tannish; venter bright yellow to pale peach color. Primary spots large, bold and well separated; secondary spots running into stripes. Black pigmentation enclosing several spots.

Coloration in life of adult male type and paratopotypes (males from series MCZ Nos. 60207-54). Very pale ash grey to tan; venters yellow to pale peach. Primary spots very large and bright; in most specimens they are blue — varying from sky blue to merely a faint blue-grey. These primary spots form two to three, occasionally four, extensive black pigment areas, corresponding to the primary spot rows. Each black patch contains from two to three primary spots and sometimes extending so far as to nearly surround the secondary spots. The secondary spots are less bright but quite bold and large and well run together, forming vertical stripes on most specimens, particularly posteriorly. The head and neck are stippled with whitish spots and streaks; the skin around the eye is the same color as this stippling. In nearly half the specimens the head has a very wine-red cast, particularly anterior to the eyes. In all cases the snout is at least browner than the ground color. (Bottom, Plate 1.)

Throat fan. Light bright yellow.

Color of females and juveniles (paratopotypes from series MCZ 60207-54). Pale grey ground color; venters yellowish. More spots and these more run together than in any other form. Dorsal and lateral striping also bolder.

Additional paratypes. MCZ Nos. 60299-317, Picard. This series, from a wetter area, is somewhat darker and more yellow than the Cabrits specimens; otherwise it agrees on all characters.

MCZ Nos. 60255-75, Pointe Ronde. These agree with the Cabrits series on all characters, but show slightly more yellow along the sides.

MCZ Nos. 60276-98, Grand Savanna. This series differs from the Cabrits specimens on no diagnostic characters, but shows a definite tendency for the bright yellow of the venter to invade the dorsal ground color — though it remains basically pale grey. There is much less evidence of red on the head anterior to the eyes, though this area is still generally browner than the rest of the ground color.

Discussion. The leeward coast of Dominica from the Grand Savanna to the Cabrits is the driest part of the island. Largely, it is truly xerophytic. This is the habitat of this palest, most boldly marked subspecies. In the wetter zones, like Picard, the population approaches the tan extreme of ground color. To the north *cabritensis* intergrades with the windward coast form (see below). Animals from the southern part of the range are brighter yellow and the yellow invades the dorsal ground color; in the northern part of the range there is a tendency toward red on the top of the head that is considerably less frequent in the southern population. In the male the heavy, bold spotting, large black pigment areas and stippling on the head and neck serve to distinguish this form immediately. Young and females are distinguished with equal ease by their pale grey ground color and large, bold markings.

This form shows the greatest degree of caudal cresting; the nuchal crest is also very well developed.

In size this seems to be the second largest — the biggest male measuring 75 mm snout to vent.

ANOLIS OCULATUS MONTANUS subsp. nov.

Type. MCZ No. 60319, Fresh Water Lake, *ca.* 2500 feet. Coll. J. Lazell, 6 July, 1959.

Diagnosis. Ground color from light to dark green; venter paler green to rather bright metallic green. Spots small and bright; primary rows with spots larger and further apart, secondary rows with spots smaller and close together. Black pigmentation in one or more patches surrounding spots of primary row.

Coloration in life of adult male type and paratopotypes (males from series MCZ 60318-37 and 65919-48). Ground color from light leaf green to dark slatey green; venter paler green and dingier. Spots in irregular but recognizable rows — those of the

primary rows may have some (one to two — occasionally three) black patches surrounding one or two of the spots on each of the anterior rows. All spots rounded in shape and from white to lime green in color. Spotting extends profusely onto the head and neck — often well onto the ventral surface. Skin around eye sea green. (Top, Plate 2.)

Throat fan. Dark yellowish suffused with rusty brown. Scales light green.

Color of females and juveniles (paratopotypes from series MCZ 60318-37). Ground color green; venter often metallic looking. Spots small and fairly profuse. Fans dark brick-red. Dorsal stripe and lateral streak usually present.

Additional paratypes. MCZ No. 60338, Gleau Gomier, at the Old Carib Trace, *ca.* 2000 feet. MCZ Nos. 60339-49, Fond Hunt, *ca.* 2000 feet. These series agree in all characters with the topotypic series.

Discussion. This form is found throughout the central mountain range in rain forests over 2000 feet, approximately, and up to nearly 3000 feet. Evidence of its genetic influence can be found in the presence of greener coloration in surrounding populations at elevations above 800 feet. From this level spotting changes clinally upward until it becomes consistent as that characteristic of the montane subspecies at about 2000 feet. It is interesting to note that no evidence of *montanus* influence exists in the specimens taken on Morne Paix Bouche, *ca.* 1600 feet, on the coast, and thus the distance inland seems to be a factor as well as the elevation itself. The northern high point of the island, Morne au Diable, provides a series taken between 2000 and 2500 feet. These animals show definite *montanus* characters, but more closely resemble the windward coast form. This highland area is separated from the main ridge of mountains on the island by a gap that is little higher than 200 feet. Specimens taken at Dos D'Ane, at the high point of the gap, *ca.* 200 feet, show no evidence of *montanus* influence; the population on Morne au Diable is thus separated from the rest of the *montanus* range and surrounded by the windward coast form and its intergrades with *cabritensis*.

In this subspecies the tail crest is usually well developed but the nuchal crest is as little in evidence as in *A. o. oculatus*.

This is certainly the largest subspecies; a number of adult males measure between 76 and 85 mm. snout to vent and one, MCZ No. 60344, from Fond Hunt, is probably the largest *Anolis oculatus* ever collected — measuring 96 mm snout to vent.

ANOLIS OCULATUS WINSTONI subsp. nov.

Type. MCZ No. 60467, Woodford Hill. Coll. J. Lazell, 29 June, 1959.

Diagnosis. Ground color coffee; venter deep peach to bright yellow. Little distinction between primary and secondary spots; spots tend to be rounded in outline and small to moderate in size. Black pigmentation rudimentary, at most dark borders to the spots.

Coloration in life of adult male type and paratopotypes (males of series MCZ Nos. 60441-90). Ground color coffee, varies from light to dark. Venter usually deep peach, sometimes shading to bright yellow. The animals are heavily peppered with small to moderate sized white dots that often have some indication of dark bordering, though never the black patches found in the other forms. There is little if any distinction between primary and secondary spot rows in most specimens. Spots extend heavily onto the head and neck; skin around eye varies from white to sky blue. (Bottom, Plate 2.)

Throat fan. Deep pumpkin yellow.

Color of females and juveniles (paratopotypes from series MCZ 60441-90). Ground color coffee, sometimes with faint olive tint. Spots less obvious than in adult males and somewhat obscured by longitudinal streaking.

Additional paratypes. MCZ Nos. 60491-507, Penville; MCZ Nos. 60508-20, Blenheim; MCZ Nos. 60640-4, Hatten Garden; MCZ Nos. 60521-4, Salybia; MCZ Nos. 60525-38, Castle Bruce; MCZ Nos. 60539-50, Rosalie; MCZ Nos. 60622-39, La Plaine. All agree with the topotypic series in all characters.

Discussion. This form has the widest range of the four, being found in the transitional forests or wet lowlands all along the windward coast from the northern point, Penville, to the barrier of Morne Paix Bouche, south of which the country becomes drier. Specimens taken at Pointe Mulatre, just north of Morne Paix Bouche, fit *winstoni* well, but are paler and more olive with spotting less distinct; this then is the zone of intergradation with the nominate form. *A. o. winstoni* intergrades with *cabritensis* at Dos D'Ane, between the central massif and Morne au Diable, and on the northern coast as far south as the Cabrits peninsula. It intergrades with *montanus* on Morne au Diable and undoubtedly all along the eastern slope of the Morne Grand Bois-Diablottin massif. Ecologically, then, this is the form of the wet lowlands.

The nuchal crest is more pronounced in *winstoni* than in any other form, though the caudal crest is not usually so well developed as in *cabritensis*. There is a tendency in old males for the scales within the white dots to become swollen and tubercular; this occurs to slight extent in both *montanus* and *cabritensis* in occasional specimens; this never occurs in *oculatus*. In no case, however, is it as pronounced or common as in *winstoni*.

In size this form falls between *oculatus* and *cabritensis*, with the largest male measuring 74 mm snout to vent.

This subspecies is named for Charles A. Winston, Manager of Woodford Hill Estate, and his family. His knowledge of the island's wildlife and his constant willingness to assist me in my wanderings over the island made possible the collection here reported.

Discussion

There are several additional series of *Anolis oculatus* which are pertinent to the discussion of this animal. These include MCZ No. 28593, Roseau; coll. Thomas Barbour, 1929. This specimen is badly faded, but shows the black pigment areas well and these would definitely relegate it to the subspecies *oculatus*. MCZ Nos. 55706-8, Roseau; coll. G. Underwood, 28 July, 1956 — also typical *oculatus*. MCZ No. 59162, near Fresh Water Lake, ca. 2000 feet; coll. Dr. Joseph Seronde, 3 July, 1959. This specimen is apparently a typical young *montanus*. Two other series present difficulty:

MCZ No. 6160 (24), Roseau; coll. S. Garman, 1879. This appears to be a series of specimens intermediate between *oculatus* and *cabritensis*, possibly from the coastal area around St. Joseph or Machouchery, eight or nine miles from Roseau. In fact, this series agrees quite well with my own from Machouchery (MCZ Nos. 60645-54) which are intermediate in characters. This area is close enough to Roseau so that it seems feasible that the series in question could have been collected there; in fact, since the large estates on the island were in this area, it seems quite probable that Garman headed in that direction. (Note that some of Cope's type series seem intermediate in the same way but to a lesser degree.)

The second series, MCZ No. 6159 (14), Portsmouth, coll. S. Garman, 1879, is more difficult to interpret. Three appear to be *winstoni* \times *montanus* intergrades, possibly from the hills to the

northeast of Portsmouth; proceeding in this direction the influence of the coastal *cabritensis* is quickly lost. Eight are so badly faded that at first they suggest *oculatus* of the south coast; this I believe is entirely due to the fading though, for where any indication of spotting remains it would indicate some head markings, making a northern locality likely. The three remaining juveniles are badly discolored and cannot be assigned to any particular form. It seems at least plausible that all of these came from the hills above Portsmouth.

Garman states in his account of these animals (1887) that they were taken "at several points on Dominica," though only two localities appear on the labels. He includes a description of them that certainly fits the species, but which cannot be assigned to any one of the subspecies.

Possibly these old collections serve to emphasize the remarkable differences that can take place on an island like Dominica within a relatively small area—literally within a comfortable walk! The island is only twenty-eight miles long and approximately seventeen miles wide and it may at first look seem strange that subspecies differentiation could take place on it at all. However, when one considers that Dominica's central highlands rise to nearly 5000 feet in several places and that the prevailing wind direction is constantly from the northeast then the wide differences that exist in habitats and ecologies become clearly explicable.

The top and windward side of the island are blanketed with rain forest nearly down to sea level, where cultivation has not cleared the original vegetation. Along the windward coast is a broad transitional zone, which gives way on the leeward coast and southern tip to semixerophytic and xerophytic dry scrub woodlands and cactus country. The coast that lies in the lee of the huge massif of Morne Diablotin is virtually deprived of any rainfall—at least by comparison with the country to the windward of it.

The floral ecology of Dominica then divides into strikingly different zones that correspond remarkably with the distributions of the four geographic races of *Anolis oculatus* (Hodge, 1954).

In summation, it seems evident that the differing ecologic zones on a single island, such as Dominica, are more effective in differentiating forms of reptile life than are barriers, like water expanses, between islands of similar ecology. We need only compare Dominica with Antigua and Barbuda in the Leeward Islands to the north: even between these islands separated by

forty miles of sea there is little if any noticeable difference in the *Anolis* population. Both are low, dry islands with only pockets of wetter vegetation. Ecologically the two are virtually the same — a far cry from the situation that obtains in moving from one side of the island of Dominica to the other.

TABLE OF DIAGNOSTIC CHARACTERS
in
Anolis oculatus Subspecies

	<i>oculatus</i>	<i>cabritensis</i>	<i>montanus</i>	<i>winstoni</i>
Throat fan color	Pumpkin yellow	Light bright yellow	Dirty reddish	Pumpkin yellow
Dorsal spotting (white)	Indistinct primaries; Secondaries mere mottling	Large, bold primaries; Secondaries bold, run together	Small, round alternating primaries and secondaries	Small, bold; little differentiation
Black pigment areas	Variable; small — 0 to 3 present	Large; extensive, 2 to 4 present	Small; 1 to 3 present	Reduced to mere dark bordering
Ground color	Olive to tan	Pale grey to tan	Green	Coffee
Venter color	Dirty yellow to white	Yellow to pale peach	Green	Peach to bright yellow
Tail crest	Low	High	Moderate	Moderate
Size (maximum) (snout to vent)	73 mm	75 mm	74 mm	96 mm

VI. SPECIES AND ECOLOGY

By ERNEST E. WILLIAMS

Anolis oculatus and its races, and the sibling pair *Anolis wattsi*—*A. alter* emphasize the strong correlation of *Anolis* species with ecology. A parallel case is provided by the brown and green races of *Anolis lineatopus* (Underwood and Williams, 1959).

It is very instructive to contrast the races of *A. oculatus* with *A. wattsi* and *A. alter*. In *A. oculatus* it is conspicuous that gene flow is even now occurring between strongly marked races adapted to sharply distinct ecologies. Relatively narrow zones of intermediate ecology permit the existence of intermediate populations that still effectively bind this heterogeneous assemblage into a single gene pool.

In the case of *alter* and *wattsi*, intermediate ecologies are absent and the thread of genetic continuity seems to be broken also. It is tempting to suppose that—by analogy with the *oculatus* races—*alter* and *wattsi* differentiated on the Antigua-Barbuda bank in wet and dry zones respectively, that with the climatic deterioration which occurred in the late Pleistocene (Richard Howard, personal communication)¹ the wet areas have been reduced to sharply set off highly peculiar disjunct oases on islands that are primarily arid. Thus *A. alter* would be confined—as it seems to be—to these singular remnants of wet forest—tiny “lost worlds.” The gene flow that had existed between the subspecies *wattsi* and the subspecies *alter* would have progressively diminished with the contraction and ultimate disappearance of the intermediate zones between wet and dry ecologies. In such a way it might be believed that *alter* and *wattsi* have achieved that genetic independence which currently appears to define their species status.

But the evidence does not at the moment permit us to exclude other possibilities. *A. wattsi* occurs not only on the Antigua-Barbuda bank but on the St. Kitts-Nevis-St. Eustatius bank and

¹ The former more favorable ecology of Barbuda is demonstrated also by the fossil fauna found there by Walter Auffenberg (1958). An extinct *Hyla* and an extinct representative of the snake *Pseudoboa* are cited by him.

on the St. Martin-Anguilla-St. Barts bank as well.¹ While *A. wattsi* may have spread out from Antigua to these other islands very recently, no present evidence negatives the alternative that it has recently invaded Antigua-Barbuda from elsewhere. In this case *A. alter* might be the autochthonous element on Antigua and Barbuda, and *A. wattsi* the invader that has seized the dry island areas that wet-area adapted *A. alter* held but weakly or not at all.

We cannot now choose among these and other hypotheses but the dominant role of ecology and ecological change in the history of *Anolis* species in the Antilles is already strongly highlighted.

¹ The occurrence on St. Lucia (Underwood, 1959) may be a case of human transport.

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